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On the Nature of the Resistance of the Potato to Wart Disease.

BY

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With Plate XIV.

THIS investigation was undertaken in the hope of throwing some light on the nature of immunity to wart disease exhibited by certain varieties of potato. The main object was to determine whether infection of immune varieties took place at all, and, if so, in what way the development of disease was stayed. An examination also was made of shoots of both immune and susceptible varieties in order to ascertain whether there were any differences, such as thickness of cuticle, wax formation, growth of hairs or any other feature which might form an obstacle to penetration by the parasite.

Examination of Uninfected Shoots.

The following varieties were examined:

Susceptible.	*Immune.*
Arran Chief.	Great Scot.
Midlothian Early.	Tinwald Perfection.
Ninety Fold.	Edzell Blue.
	Kerr's Pink.

Only very young shoots, less than $\frac{1}{4}$ in. high, were used, hand sections being made from fresh material and microtome sections from material fixed in Flemming's solution. A variety of cuticle stains were tried: scharlach red in 70 per cent. alcohol, sudan III, ammoniacal fuchsin, and chlorophyll, freshly extracted in alcohol. Of these four, scharlach red was found to give the most satisfactory results, staining the cuticle a faint red; this showed more clearly when lichtgrün was used as a counter stain. No anatomical differences were observed between the two sets of shoots and no difference in staining reactions could be detected between the cuticle of susceptible and immune varieties; in fact, very little cuticle appeared to

have been formed, and none could be detected at the extreme apex, although, Lee and Priestley[1] states, that cuticle is present over all growing points.

The epidermal wall varied in thickness in the same variety, some sections showing quite a thick epidermal wall and others a comparatively thin one. The thickness also varied with the distance from the growing point where the wall was always very thin.

Schultz macerating fluid was found very useful in showing the structure of the wall, causing a swelling of the cellulose layer, and showing the cuticle as a barely perceptible brown line with slightly thickened pegs at the juncture of the cells.

Inoculation.

Method. The inoculations were made with zoospores from summer sporangia, using pieces of young warts in which the sori were already in the process of bursting. The method adopted was practically the same as that used by Miss Curtis.[2] She found Sphagnum moss to be a good substitute for soil, being cleaner to work with. In the present investigation, however, better results were obtained by using soil, the percentage of successful results with susceptible varieties being 70 per cent. with soil, as against 2 per cent. when Sphagnum was employed. The tubers were potted up in light garden soil, leaving the top shoots uncovered. Small pieces of fresh wart were placed, sorus side down, on the tips of the young shoots and a drop of water added. The soil was carefully placed round the shoot to hold the piece of wart in position, after which the whole was covered with soil and well watered.

The pots were placed for two days in shallow dishes containing water to ensure the soil being thoroughly saturated; after this time they were kept moist by watering from time to time.

Effect of Temperature.

Rough experiments were made to see if the temperature at which the tubers were kept had any effect on infection.

Tubers were divided into batches A and B, and sprouted at 15·6° C. (60° F.) and 26·7° C. (80° F.) respectively. They were then inoculated, and after inoculation batch A was subdivided, half being kept at 15·6° C. (60° F.) and half at 26·7° C. (80° F.); batch B was similarly treated.

For the high temperatures the tubers were kept in an incubator at constant temperature; for the lower temperature they were kept in a potting room having a temperature approximately 60° F. The tubers grown in an

[1] Ann. Bot., vol. xxxviii, p. 525, 1924.
[2] Phil. Trans. Roy. Soc., B., vol. ccx, p. 409, 1921.

incubator at 80° F. sprouted very rapidly; those grown in the cold less rapidly.

It was found that sprouting at a high temperature, before inoculation, gave better results than sprouting at a low temperature; but, on the other hand, tubers kept at the high temperature grew too fast after inoculation, and produced weak and sickly looking shoots giving a comparatively low percentage of infection. The rate of growth of the parasite itself was increased with a rise of temperature, young warts showing on the seventh day after inoculation instead of on the tenth, as is the case at low temperatures.

The best infections were obtained with shoots grown previous to inoculation at 80° F. and kept after inoculation at 60° F. and under as normal conditions as possible.

On the whole the parasite was found to be very little susceptible to change of temperature. Infections were obtained at temperatures varying from 58° to 80° F. The heaviest infections were obtained at temperatures of about 60° F. and under conditions most conducive to healthy growth of the tuber.

The results of these experiments are tabulated below:

Inoculations at high temperatures, 25·6°–26·7° C. (78–80° F.)

	No. of Inoculations made.	*No. of successful Inoculations.*	*% of Success.*	*Mean % of Success.*
Potatoes sprouted in cold room.	67	15	22·4	23
Potatoes sprouted in incubator.	77	18	23·4	

Inoculations at low temperatures, 14·4°–17·8° C. (58–64° F.)

	No. of Inoculations made.	*No. of successful Inoculations.*	*% of Success.*	*Mean % of Success.*
Potatoes sprouted in cold room.	114	75	65	68
Potatoes sprouted in incubator.	141	100	80	

Infection of an Immune Variety.

Parallel series of inoculations were made on an immune (Great Scot) and on a susceptible (Arran Chief) variety, care being taken that the conditions under which the two sets of inoculations were made should be as similar as possible. The inoculations were made at the same time, using material cut from the same piece of wart. After the required length of time the shoots of Great Scot were cut and fixed simultaneously with some of the

shoots of Arran Chief. The rest of the shoots of Arran Chief were left to act as controls, the development of warts being taken as an indication of the success of the inoculation. It was considered useless to examine the fixed material unless the controls gave a high percentage of infection. The fixative used was Flemming's strong solution diluted with water to half its strength. For staining gentian violet and orange G. were usually employed and occasionally Heidenhain's iron-alum-haematoxylin.

In the sections of the shoots of Great Scot not only were zoospores found fixed to the surface of the epidermis (Pl. XIV, Fig. 1), but others were to be observed passing through the cuticle and outer wall of the epidermal cells (Pl. XIV, Figs. 2–7). In one case a zoospore was seen half-way through the wall, the part inside being connected with the part outside by a fine thread very darkly staining and showing all the more clearly because of the thickness of the wall; Pl. XIV, Fig. 5 shows the strand through the wall running to the nucleus of the zoospore. Pl. XIV, Fig. 8 shows the zoospore immediately after entry.

Comparison of these sections with sections through similar infected material of Arran Chief (Pl. XIV, Figs. 13–16) showed beyond doubt that these were zoospores of *Synchytrium endobioticum* penetrating the tissues of the variety Great Scot; they agreed in size and method of penetration with those figured by Miss Curtis. Material of Great Scot fixed three days after inoculation showed inclusions in the cells with every appearance of being the parasite reduced in size and apparently becoming disorganized (Pl. XIV, Figs. 9–11). These inclusions had a definite structure consisting of a reticulated body with a distinct nucleus surrounded by a clear space. The reticulated part was shrunken and appeared to be in process of dissolution. The nucleus was small in size and sometimes faintly staining. In no case was the parasite found in any later stage of development, and no warts were seen. The parasite apparently dies after entry without bringing about the death of the host-cell.

It is evident that immunity to wart disease, at least in the variety Great Scot, does not depend on a capacity to keep the invader out, but is mainly or wholly due to some physiological characteristic of the cells which render them unsuitable for the further development of the parasite. In the present state of our knowledge it is hardly profitable to speculate on the nature of this characteristic.

Summary.

There is no anatomical difference between the young shoots of varieties of potato respectively immune and susceptible to wart disease.

Changes of temperature had very little effect on the degree of infection. Infections were obtained from temperatures varying from 58° to 80° F.

The healthiest tubers took the disease most readily. The most satisfactory infections were made with tubers kept under normal conditions.

Zoospores of the parasite are capable of penetrating the epidermal cells of young shoots of the immune variety Great Scot. For the first two days the development of the organism in immune varieties seems normal: the organism increases in size and travels down the cell in the same manner as it does in susceptible varieties. After that time it becomes smaller and less definite in outline, showing signs of disorganization. It appears finally to become dissolved and so disappears from the host-cell.

The resistance of the immune variety Great Scot is not due to a capacity to prevent the entry of the invading parasite, but to some physiological characteristic of the epidermal cells which brings about the death of the invader after entry.

This work was undertaken at the suggestion of Professor V. H. Blackman, whom I wish to thank for kindly criticism.

DESCRIPTION OF PLATE XIV.

Illustrating Mrs. K. Cartwright's paper on the Nature of the Resistance of the Potato to Wart Disease.

Figs. 1–8. Stages of infection of the epidermis of the immune variety Great Scot.

Fig. 1. Zoospore on surface with cilium partly retracted. The host-cell cytoplasm shows a dark staining mass just opposite the zoospore. × 1,625.

Fig. 2. Early stage of penetration; section slightly oblique. × 1,625.

Fig. 3. The upper zoospore shows a peg-like structure connected with the nucleus, penetrating the cell-wall. The nuclear contents of the lower one are within the cell. × 1,500.

Fig. 4. An indication of a thread-like structure connected with the nucleus of zoospore is to be seen through the cell-wall. × 1,750.

Fig. 5. A dark staining thread is clearly seen penetrating the cell-wall. × 2,000.

Fig. 6. Host-cell cytoplasm contracted; the thread-like structure is very clearly shown. × 1,400.

Fig. 7. Part of the contents of the zoospore is to be seen inside the host-cell connected to the nucleus of zoospore by a fine thread. × 1,833.

Fig. 8. Penetration complete; the zoospore is inside the host-cell. × 1,700.

Figs. 9–12. Later stages, showing the parasite inside the tissues of the variety Great Scot.

Fig. 9. The parasite shows an irregular outline and reticulated structure; has not yet passed the host-nucleus. × 1,700.

Figs. 10–12. Later stages with the parasite at the base of the epidermal cell and showing an irregular outline. × 1,700.

Figs. 13–16. Stages of penetration into the susceptible variety Arran Chief.

Figs. 13–15. Stages of penetration. × 1,850.

Fig. 16. Two of the parasites in one cell of Arran Chief. The more regular outline of the organisms as compared with those of Figs. 9–12 is to be noted. × 1,475.

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